Parasite species richness and intensity of interspecific interactions increase with latitude in two wide-ranging hosts

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Abstract. Although the latitudinal diversity gradient is a well-known and general pattern, the mechanisms structuring it remain elusive. Two key issues limit differentiating these. First, habitat type usually varies with latitude, precluding a standardized evaluation of species richness. Second, broad-scale and local factors hypothesized to shape diversity patterns co-vary with one another, making it difficult to tease apart independent effects. Examining communities of parasites in widely distributed hosts can eliminate some of these confounding factors. We quantified diversity and interspecific interactions for trematode parasites infecting two similar snail species across 27 degrees of latitude from 43 locations in tropical and temperate oceans. Counter to typical patterns, we found that species richness, levels of parasitism, and intensity of intraguild predation increased with latitude. Because speciation rates are precluded from driving diversity gradients in this particular system, the reversed gradients are likely due to local ecological factors, specifically, increased productivity and stability. We highlight how this system may serve as a useful tool to provide insight into what processes drive diversity gradients in general.

Key words: biotic interactions; dispersal; diversity patterns; intraguild predation; latitudinal gradients; parasites; rarefaction; species richness; trematodes.

Introduction

Perhaps the greatest challenge to understanding why there are more species in the tropics compared to temperate regions has been that many of the proposed mechanisms for the well-known latitudinal diversity gradient (LDG) co-vary with one another and are likely not mutually exclusive (Rohde 1992, Willig et al. 2003, Mittelbach et al. 2007). It would therefore be helpful to examine the LDG for systems that, by their nature, preclude some groups of proposed mechanisms from possibly driving diversity patterns. Similar to a gene knockout experiment, the results of such a study would provide insight into the forces that underlie the LDG, no matter the results. For instance, if an LDG was not observed, this would suggest that the excluded mechanisms are important in driving the general LDG. Alternatively, if an LDG was still observed, it would provide evidence against the importance of the excluded mechanisms, and a smaller pool of potential mechanisms would remain to be considered. Here, we examine the diversity of parasites that infect widespread host species that span tropical and temperate latitudes in the Pacific and Atlantic Oceans. We posit that this system

can serve as a tool for elucidating general principles concerning the LDG because it precludes the operation of several explanatory factors.

Most functional explanations for the latitudinal diversity gradient can be at least crudely placed into two different categories (Huston 1999, Harrison and Cornell 2008). First, there are mechanisms that involve evolutionary or historical processes that operate at relatively large temporal and spatial scales. Examples of large-scale mechanisms include greater rates of speciation (e.g., given higher temperature and insolation [Rohde 1992]) and lower rates of extinction at lower latitudes (reviewed by Mittelbach et al. 2007). Secondly, there are ecological mechanisms that can operate at both relatively large and small spatial and temporal scales. For example, the "species–energy" hypothesis (also known as the "productivity" or "more individuals" hypotheses [Brown 1981, Wright 1983, Currie et al. 2004]) proposes that tropical ecosystems have more species because greater tropical productivity supports a larger aggregate pool of individuals. This larger group of individuals can be partitioned into a greater number of species that can maintain viable population sizes. A major challenge with testing various hypotheses is that many proposed mechanisms are not mutually exclusive, and that they frequently co-vary with each other and with latitude. Hence, if it were possible to examine systems that preclude the functioning of some groups of

proposed mechanisms, we could perhaps more clearly determine the mechanisms underlying the LDG.

Another difficulty with determining the patterns and mechanisms underlying the LDG is the variability in the types of habitat and resources across latitudes. In fact, it has long been hypothesized that a substantial part of the LDG may be driven by the tropics having a greater variety of habitats or resources (MacArthur 1965, Brown 1981). If we were to control for habitat and resource variability, would we still observe the LDG? Although work documenting the LDG at local scales (alpha richness) does provide some control of habitat and resource variability, there is still uncertainty concerning the importance of heterogeneity. Experimental manipulation using artificial habitat patches (e.g., Freestone and Osman 2011, Freestone et al. 2011) is one way to control for this. Another way to control both habitat and resource variation is to examine widespread host species infected with specific parasites, because of the natural standardization they can provide.

Hosts provide naturally replicated, standardized habitat and resource units for communities of parasites (Holmes and Price 1986, Price 1990, Hechinger 2013). Therefore, a widely distributed host species could provide a high degree of standardization of habitat and resource type across latitudes. Additionally, for some hosts it is feasible to sample numerous populations, providing high replication of local parasite communities throughout the latitudinal range. Hence, the feasibility of rigorous sampling and habitat/resource standardization provided by communities of parasites specialized on broadly distributed hosts suggests that they can provide powerful systems for understanding latitudinal diversity gradients. Despite this, we are aware of no previous studies examining parasite diversity in a single species spanning the temperate zone to the tropics (other than humans, see *Discussion*).

Diverse communities of trematode parasites infect and castrate the Pacific horn snail, *Cerithideopsis californica* (=*Cerithidea californica*, see Reid and Claremont 2014) and the Atlantic horn snail, *Cerithideopsis pliculosa* (=*Cerithidea pliculosa*) (Martin 1972, Wardle 1974, McNeff 1978, Hechinger et al. 2007). These snails are sister species that diverged from one another following the formation of the Isthmus of Panama (Miura et al. 2010). The two snail species are each broadly distributed in respective oceans, from the tropics to the temperate zone (Keen 1971, Warmke and Abbott 1975, Miura et al. 2012). The snails are common and often very abundant in intertidal mangrove and mudflat habitats. These habitats are major foraging areas for migratory shorebirds, which serve as final hosts for the trematodes and disperse them widely along their flyways (e.g., Miura et al. 2006). Thus, these trematode parasites have several useful attributes for examining latitudinal diversity gradients. First, the broadly distributed snail hosts serve as a standardized habitat and resource type across latitudes. Second, the

use of widely ranging migratory birds as final hosts permits the rapid dispersal of trematodes over thousands of kilometers to different snail populations across latitudes (Miura et al. 2006). This rapid and wide dispersal of species among latitudes should remove the signature of regional-scale processes, such as oceanic current dispersal boundaries, latitudinal variation in the composition of species pools, or latitudinal variation in speciation rates. Supporting this idea, the known geographic ranges of most of these trematode species span the ranges of their hosts, from tropical to temperate latitudes in both Pacific and Atlantic Oceans (Fig. 1). Combined, these attributes permit focus on how local (vs. broad-scale) ecological factors contribute to latitudinal diversity gradients.

In addition to species richness, current, albeit limited, evidence suggests that the intensity of interspecific interactions also increases towards the tropics (see review by Schemske et al. 2009, and Freestone et al. 2011). Indeed, the biotic interactions hypothesis proposes that strong species interactions in the tropics increase diversification rates, leading to high diversity at low latitudes (Dobzhansky 1950, Mittelbach et al. 2007, Schemske et al. 2009). Additionally, higher diversity could lead to increased opportunities for interspecific interactions to occur. While measuring interspecific interactions in free-living species presents several challenges, trematode parasitic castrators enable straightforward examination of the intensity of interspecific interactions, and do so in two different ways. Most simply, we can directly measure the level of parasitism in host populations across latitudes (e.g., proportion of snails infected and castrated by trematodes). Additionally, we can examine interactions between the parasite species themselves. These trematodes strongly interact through a form of intraguild predation that follows a well-defined dominance hierarchy (Kuris 1990, Sousa 1993, Lafferty et al. 1994, Hechinger 2010). When two trematode species encounter each other in the same host, the dominant species predictably kills (excludes) the subordinate species, most often by eating it. Importantly, it is possible to estimate the number of individuals lost to intraguild predation using observed abundance information (Lafferty et al. 1994). Because the dominance hierarchy is known for these species, and is based on gross morphological characters (e.g., body size) that are stable throughout our study area (R. F. Hechinger and M. E. Torchin, *personal observations*), it is also possible to quantify the intensity of intraguild predation across latitudes.

Here, we examine trematode species richness and interaction intensity in populations of two horn snail species from temperate North America to tropical southern Central America in both the Atlantic and Pacific Oceans. We hypothesized that if broad-scale factors or habitat/niche variability were the primary drivers of the LDG, we would not see a typical decrease in diversity with latitude. However, if local ecological
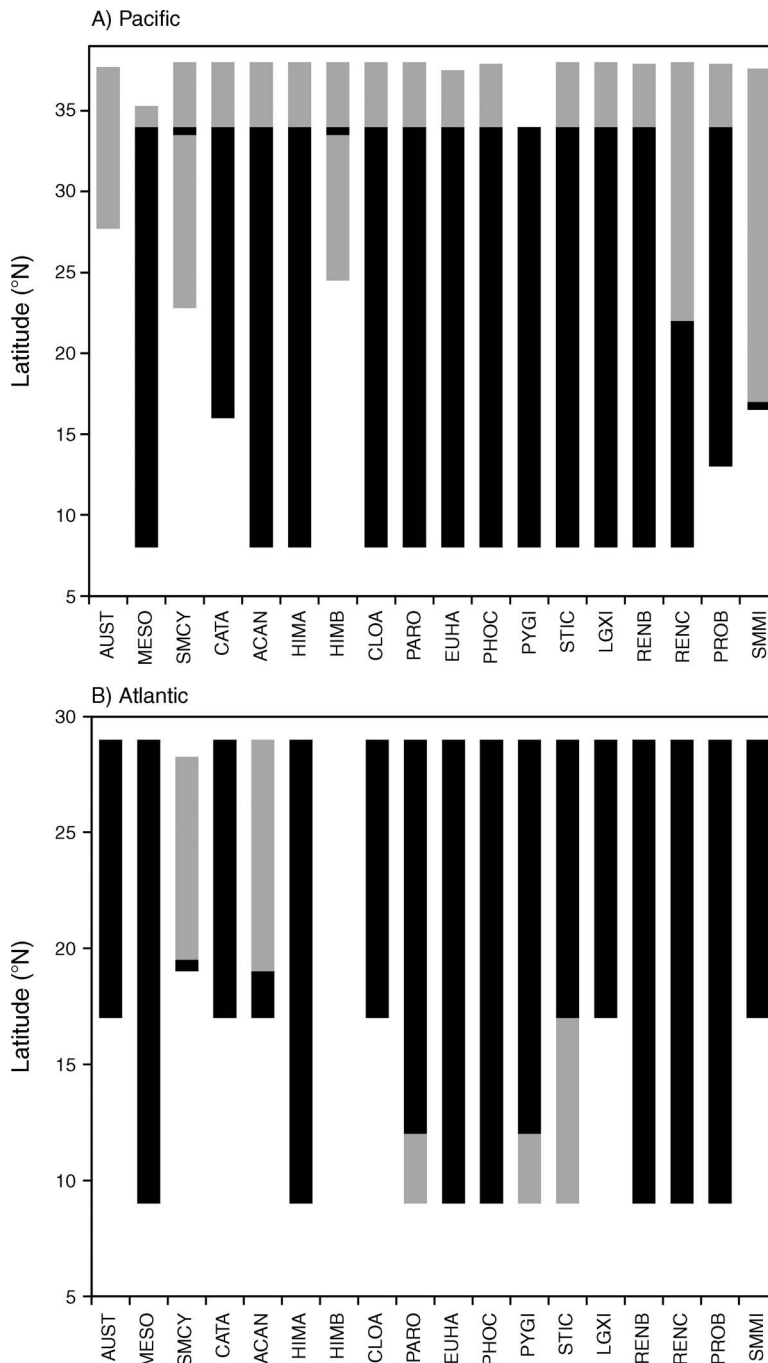
Fig. 1. Latitudinal ranges for the trematode species comprising the guild of parasitic castrators that infect the (a) Pacific (*Cerithideopsis californica*) and (b) Atlantic (*C. pliculosa*) horn snails. The *x*-axis labels are trematode species codes (see Appendix B for species names). Black bars indicate species ranges recovered by sampling in the current study, while gray bars indicate the broader ranges known by using information from additional sampling by the authors, Wardle (1974) and J. C. Buck (*personal communication*). The data indicate that most or all species are found throughout the entire range of their habitat (host snails), as expected given the wide dispersal provided by migratory birds. Local richness is likely a result of ecological factors influencing species' abundances.

factors are important in driving diversity gradients, we would see an LDG. Consistent with this, we also hypothesized that the intensity of interspecific interactions would track species diversity gradients. We found

that, in contrast to general patterns, trematode species richness in both snail species was positively correlated with latitude, exhibiting a "reversed" LDG, where the tropics are relatively low in trematode species richness
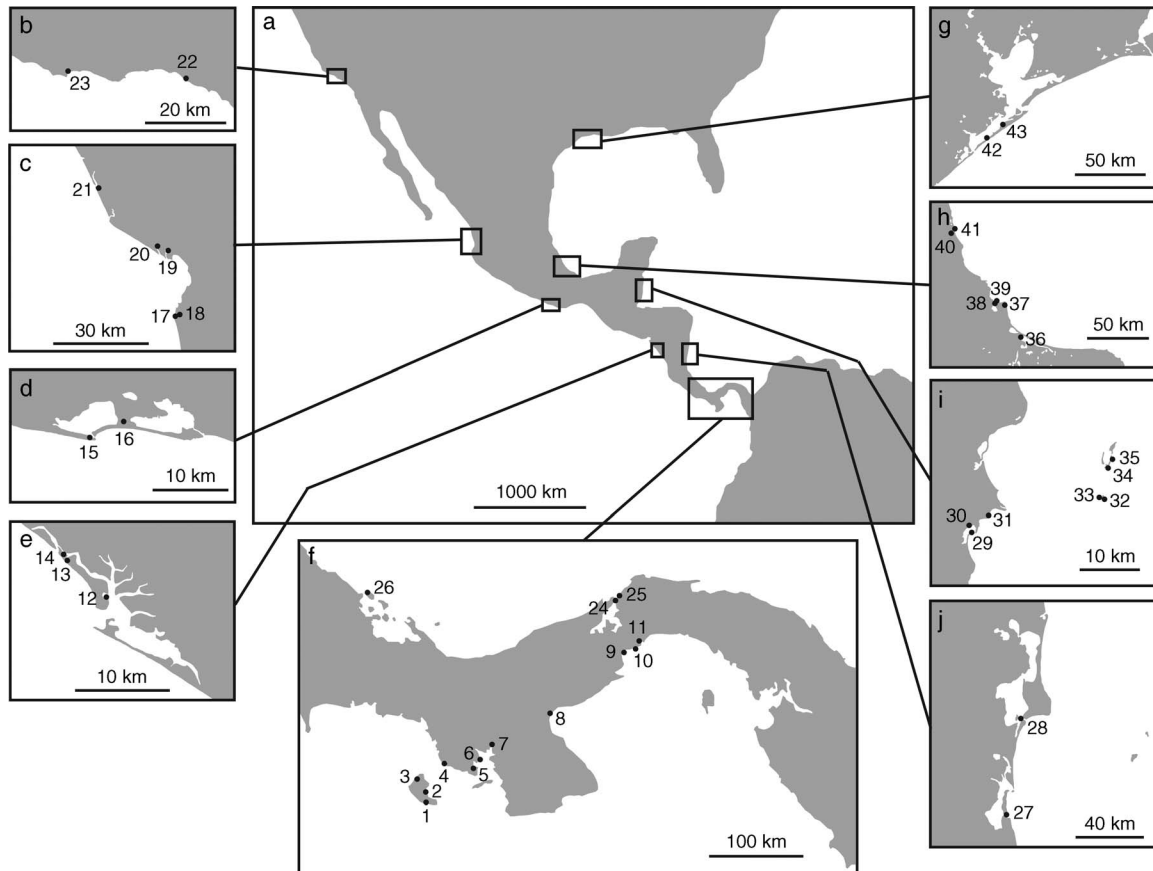
FIG. 2. Location of sampling sites throughout North and Central America (a) entire region; (b) Santa Barbara, California; (c) Nayarit, Mexico; (d) Oaxaca, Mexico; (e) Nicaragua; (f) Panama; (g) Galveston, Texas; (h) Veracruz, Mexico; (i) Belize; and (j) Nicaragua.

compared to temperate regions. Further, consistent with this reversed latitudinal pattern, we found that the strength of interspecific interactions, measured as the intensity of intraguild predation, also increased from low to high latitudes.

MATERIALS AND METHODS

Data collection

We sampled snails across 27° of latitude along both coasts of North and Central America, covering most of the geographic distribution of both Pacific and Atlantic horn snails, *Cerithideopsis californica* and *C. pliculosa*, respectively. We note that, given the molecular genetic evidence in Miura et al. (2010), we consider *C. californica* to include the nominal species: *C. californica* (Haldeman), *C. mazatlanica* (Carpenter), and *C. valida* (Adams). In the eastern Pacific, our southernmost sampling locations correspond to the peak of nearshore molluscan diversity and sea surface temperature (Roy et al. 1998, Valdovinos et al. 2003), which is shifted slightly to the north of the equator. We collected snails from 43 locations within five countries in North and Central America. However, to standardize sampling effort,

prevalence analyses included only sites for which we were able to dissect at least 100 snails, and parasite species richness analyses included those sites where we encountered at least 100 trematode infections (see *Species richness and prevalence*). Sampling locations were selected using Google Earth and previous experience to identify suitable estuarine habitats for snails. From January 2007 through March 2010, at each location we used a standard searching procedure for horn snail populations at several sites (each <200 m²) by first identifying suitable habitat and then searching for snails (generally within mangrove roots or near salt marsh vegetation). Most sites were located in different estuaries, but in a few cases sites in the same large system were separated by a few kilometers (Fig. 2; Appendix A). We treated sites as independent samples for our analyses, because these snails have very low mobility, and trematode diversity varies over small spatial scales (Hechinger and Lafferty 2005, Torchin et al. 2005, Hechinger et al. 2007). We targeted the largest snails from each site for dissections, as these are generally older and have a higher probability of being infected with parasites (e.g., Kuris 1990, Sousa 1993, Torchin et al. 2005).
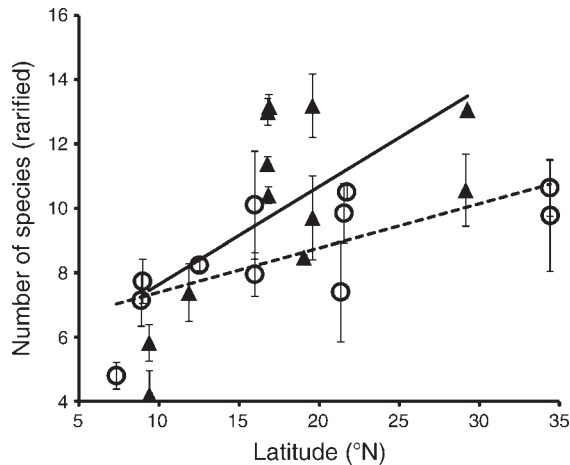
FIG. 3. Species richness (mean ± SD) of trematode parasites vs. latitude in the Pacific horn snail, *Cerithideopsis californica* (dashed line and open circles) and the Atlantic horn snail, *Cerithideopsis pliculosa* (solid line and solid triangles). Regression lines are fit separately for each ocean. Species richness was rarified (see *Methods and materials: Species richness and prevalence*).

Snails were measured from the apex of the spire to the apertural base with Vernier calipers and processed for parasites following Torchin et al. (2005). Trematode species were identified following Martin (1972) and R. F. Hechinger and T. C. Huspeni (*unpublished manuscript*). While we use the same morphospecies codes for both Pacific and Atlantic horn snail trematodes (Fig. 1; Appendix B), we recognize that the Atlantic species may actually be very similar cryptic species.

Species richness and prevalence

We used rarefied species richness estimates to control for sampling effort (Sanders 1968, Gotelli and Colwell 2001, Colwell et al. 2012) of trematodes by rarifying parasite species richness to a sample size of 100 trematode infections from each site using Estimates 9.10 (Colwell and Elsensohn 2014). We used a general linear model (GLM) to analyze the effect of latitude, ocean (Atlantic, Pacific) and their interaction on species richness. We used the same approach to evaluate the association of prevalence (proportion of snails infected per site) with snail size and latitude from sites where we collected and dissected >100 snails (either infected or uninfected). GLMs were made using JMP version 10 (SAS 2012).

Intensity of interspecific interactions

To measure the intensity of intraguild predation among trematode species, we estimated the total proportion of trematode infections killed by other species at each site using the formulas in Lafferty et al. (1994). These formulas require information on the trematode species dominance hierarchy, which was first constructed by Kuris (1990). We used the most recent version of this hierarchy, as presented in Hechinger (2010). The formulas estimate the number of recruited parasites killed by other trematodes by applying the observed prevalence of each species in "dominant-free" snails to the portion of the snail population infected by dominant trematodes. This prevalence, minus observed co-infections with dominants, represents the amount of trematode infections killed via intraguild predation. We summed the killed and observed infections across all species to obtain the total amount of recruits for a study site and calculated intensity of intraguild predation as the proportion of total recruits lost to intraguild predation. We then used a GLM to examine the strength of intraguild predation vs. latitude, ocean, and their interaction.

Results

Species richness and prevalence

We quantified parasitism in >27 000 snails from 43 locations within five countries in North and Central America across 27° of latitude in both the Pacific and Atlantic Oceans. Parasite species richness was greater in the temperate zone, increasing with latitude from ~7° to 30°–35° in both the Pacific and Atlantic Oceans ($F_{1,19} = 14.7$, $R^2 = 0.48$, $P = 0.0011$, Fig. 3). There was a marginally significant effect of ocean ($F_{1,19} = 3.7$, $P = 0.069$), but no significant interaction between ocean and latitude ($F_{1,19} = 2.1$, $P = 0.16$), indicating that a single slope could explain the diversity–latitude relationship in both oceans (Fig. 3).

Prevalence, or the proportion of infected snails, also increased with latitude in both oceans ($F_{1,32} = 23.7$, $R^2 = 0.52$, $P < 0.0001$, Fig. 4). There was no significant ocean effect ($F_{1,32} = 2.3$, $P = 0.14$), nor interaction
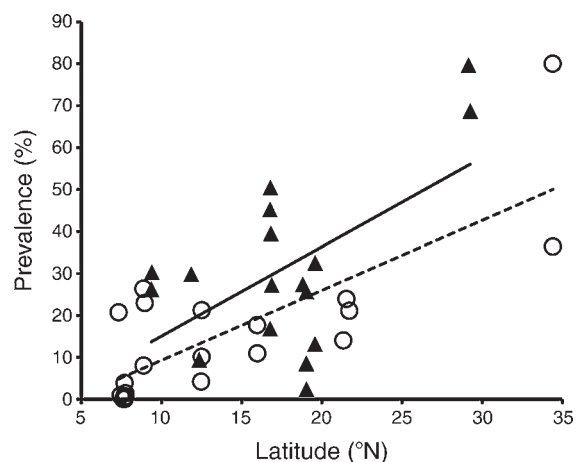

FIG. 4. Trematode prevalence (percentage of snails infected) vs. latitude in the Pacific horn snail, *Cerithideopsis californica* (dashed line and open circles) and the Atlantic horn snail, *Cerithideopsis pliculosa* (solid line and solid triangles). Regression lines are fit separately for each ocean. Data include only sites where $N \geq 100$ snails dissected.
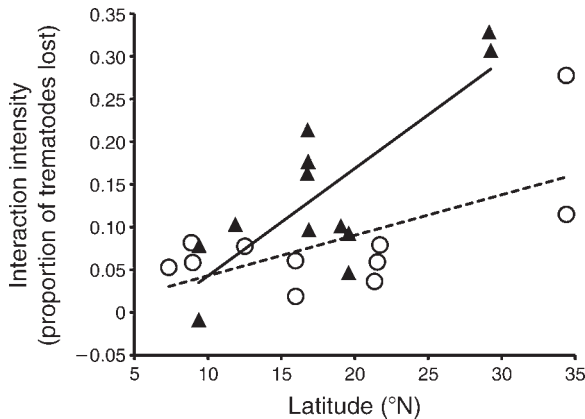
FIG. 5. Intensity of interspecific interactions (proportion of trematodes lost to intraguild predation) vs. latitude in the Pacific horn snail, *Cerithideopsis californica* (dashed line and open circles), and the Atlantic horn snail, *Cerithideopsis pliculosa* (solid line and solid triangles). (See *Methods: Intensity of interspecific interactions*.) Regression lines are fit separately for each ocean. Data only include sites where $N \geq 100$ infected snails.

between ocean and latitude ($F_{1,32} = 0.22$, $P = 0.64$). Although prevalence increased with latitude, a GLM incorporating prevalence as a predictor indicated that it did not influence the effect of latitude on species richness in either ocean ($F_{1,18} = 0.68$, $P = 0.42$; $F_{1,18} = 0.10$, $P = 0.75$ interaction). That is, species richness increased with latitude, regardless of the increase in prevalence.

Mean shell size was greater in the Pacific compared to Atlantic ($F_{1,31} = 44.6$, $P < 0.0001$) but did not consistently vary with latitude in either ocean ($F_{1,31} = 1.4$, $P = 0.23$; interaction $P = 0.30$), nor did mean size influence species richness in either ocean (main effect $F_{1,17} = 0.38$, $P = 0.54$; interaction $F_{1,17} = 2.1$, $P = 0.16$).

Intensity of interspecific interactions

The intensity of interspecific interactions, measured as intraguild predation, also increased with latitude ($F_{1,19} = 24.7$, $R^2 = 0.62$, $P < 0.0001$, Fig. 5). Here, all effects were significant (ocean, $F_{1,19} = 6.4$, $P = 0.02$; interaction, $F_{1,19} = 5.1$, $P = 0.037$), reflecting that interaction intensity increased more strongly in the Atlantic than in the Pacific. In both oceans, at low tropical latitudes, <5% of trematode recruits were estimated to be lost to intraguild predation, while this percentage increased to ~15% in the Pacific and ~30% in the Atlantic in the temperate zone. As expected, prevalence and species richness combined explained a substantial amount of the variation in intraguild predation ($R^2 = 0.94$, $P < 0.0001$, $n = 23$), and both maintained independent effects in the model (prevalence, $F_{1,20} = 218.5$, $P < 0.0001$; richness, $F_{1,20} = 8.1$, $P = 0.0098$), with no interaction between the two ($F_{1,19} = 0.43$, $P = 0.52$).

DISCUSSION

Counter to typical species diversity patterns, trematode species richness in two congeneric marine snails increased from the tropics to the temperate zone across 27° of latitude in both the Pacific and Atlantic oceans. Trematode prevalence (proportion of snails infected) was also greater at higher latitudes. Consistent with these reversed latitudinal patterns, we found that the strength of interspecific interactions, measured as the intensity of intraguild predation, also increased from low to high latitudes. Below, we (1) provide possible explanations for the observed reversed gradients of parasite species richness and intensity of interspecific interactions, (2) highlight how parasites can serve as useful tools for examining general mechanisms underlying LDGs, and (3) discuss implications of our results for understanding global patterns of parasite diversity.

Possible explanations for the reversed LDGs

Parasite species richness.—In our study, the rapid and widespread dispersal of trematodes by birds (e.g., Miura et al. 2006) precludes broad-scale factors from driving the reversed LDGs. Hence, we postulate that the reversed LDGs for these trematodes are driven by local ecological factors such as demographic attributes of the host snail populations (the primary resource and habitat for these trematodes). Our preliminary observations suggest that, at lower latitudes, the horn snail populations are characterized by greater spatial patchiness, greater mortality rates, greater temporal instability (stochastic population persistence), and potentially smaller populations. For instance, we compiled independent qualitative observations from two of us (M. E. Torchin and O. Miura, *personal observations*) concerning the density and patchiness characterizing the horn snail populations at each of the study sites. GLM analyses of these data suggest that, indeed, densities increased and patchiness decreased by about an order of magnitude at our highest-latitude study sites compared to those in the lowest latitudes (Appendix C).

These demographic attributes of the host snails could drive lower trematode recruitment rates, higher mortality rates, and higher rates of local extinction. Any of these factors would result in local diversity of trematodes being lower in the tropics compared to the temperate zone, supporting the idea that snail demographic changes may explain the reversed LDG. Aguirre-Macedo et al. (2011) document how trematode parasite diversity dropped and then slowly recovered over a few years following a major disturbance (a hurricane wiped out a local population of *C. pliculosa* in the Yucatan Peninsula, Mexico). Such greater environmental instability and habitat turnover (snail mortality) in the tropics could prevent parasite diversity from reaching the high levels characterizing temperate zone communities. Future research carefully examining infection rates (recruitment), host density (resource abundance), and host mortality (turnover) would

provide strong tests of mechanisms driving the observed reversed LDGs.

Another potential explanation, which we discount, is that variation in trematode diversity could be fueled by other hosts in the trematodes' complex life cycles (usually two additional hosts: birds as final hosts, and benthic invertebrates or fishes as second intermediate hosts). Because the diversity and abundance of these additional hosts correlates with species richness and prevalence of trematodes infecting horn snails at small spatial scales (Smith 2001, Hechinger and Lafferty 2005, Hechinger et al. 2007), these final and second intermediate hosts might drive some of the observed diversity patterns. However, both bird and second intermediate host richness are likely greater in the tropics, considering general diversity patterns in the ocean (Hillebrand 2004, Roy and Witman 2009). Hence, if trematode latitudinal diversity tracked the diversity of potential second intermediate and final hosts, it would likely lead to patterns opposite to the observed reversed latitudinal diversity gradients.

Intensity of interspecific interactions.—Consistent with the typical pattern of high diversity at low latitudes, available studies suggest that interspecific interactions are also stronger in the tropics (Schemske et al. 2009, Freestone and Osman 2011, Freestone et al. 2011). In fact, in their review, Schemske et al. (2009) could not find a single study indicating stronger interactions in the temperate zone compared to the tropics. In contrast to this general trend, our data for trematodes infecting horn snails indicated that interspecific interactions increase with latitude in both oceans, and that they do so in two different ways.

First, the proportion of horn snail hosts infected (and castrated) by trematodes was higher in the temperate zones of both oceans. This is counter to the general trend where levels of interactions, including levels of parasitism, tend to be higher in the tropics (Schemske et al. 2009). For instance, Salkeld et al. (2008) show that blood parasite loads (but not prevalence) in lizards are higher in the tropics. Similarly, Robar et al. (2010) indicate that there is a general trend for parasite-induced mortality to be greater at lower latitudes. Although trematode parasitism does not result in death of infected horn snails, infected individuals are castrated and reproductively dead, and this happens more frequently at higher latitudes.

Second, our results also indicate that the intensity of intraguild predation among trematodes increases 3–6 fold at higher latitudes. This was expected considering the reversed latitudinal gradient observed for trematode species richness and prevalence, key determinants for intraguild predation in this system; the different species cannot kill one another if they do not co-occur in the same individual snail. The probability of such interspecific encounter increases with species richness and as the proportion of habitat occupied (prevalence) increases. Although readily explainable, this result is noteworthy,

as it is contrary to general trends, consistent with the reversed LDGs. Interestingly, unlike the biotic interactions hypothesis, which proposes that strong species interactions cause diversification (Dobzhansky 1950, Mittelbach et al. 2007, Schemske et al. 2009), the observed increase of intraguild predation is most likely a consequence of greater species richness and prevalence. However, while intraguild predation does not drive the reversed LDGs, it could have influenced the shape of the reversed gradient. Specifically, intraguild predation could decrease rarer species below detection limits disproportionally in the temperate zone. In other words, the reversed LDG is potentially stronger than it appears.

Using parasite LDGs to inform general principles

We propose that additional examination of parasitism across latitudes can help reveal mechanisms driving the general LDG. For example, both mortality of individual host snails and extinction of host snail populations can be considered to represent habitat disturbance or turnover, and disturbance is one of the oldest proposed general mechanisms for the LDG, with lower disturbance fostering greater diversity (Dobzhansky 1950). Further, because snail populations are the sole resource for these trematode communities, the standing stock biomass or productivity of the snail populations, not ecosystem primary productivity, represents the energy relevant to the popular species–energy hypothesis. (See Brown 1981, who noted the importance of focusing on the appropriate pool of energy when testing the species–energy hypothesis.) Because attributes of the snail populations are both readily quantifiable and readily expressed in general terms, this system is particularly amenable to further experimental testing of hypotheses concerning the role of local factors in driving the general LDG.

There are two previously reported reversed LDGs that are relevant here. Both ichneumonid wasps (which are parasitoids of insects [Owen and Owen 1974]) and aphids (which are pathogens on plants) (Dixon et al. 1987), also appear to be less diverse in the tropics (but see Quicke [2012] who questions this pattern for ichneumonids). The "resource fragmentation hypothesis" has been proposed to explain these "reversed" patterns (Kindlmann et al. 2007). The idea is that increased host diversity in the tropics results in smaller or more fragmented host population sizes, which in turn support fewer numbers and species of specialist consumers in the tropics. The underlying mechanism behind the resource fragmentation hypothesis appears to be similar to one of the explanations we posited above: host populations represent the relevant energy pool (resource base) for the specialist species under consideration, and those pools may be smaller or more patchy in the tropics, driving lower recruitment rates or smaller population sizes, thereby supporting lower diversity. However, the above studies examine the LDG at the aggregate taxon level over all possible host species, vs. a

single host species (as with the trematodes studied here). Further, the scale of recruitment by broadly dispersing trematodes in our study contrasts with the small spatial scale over which both ichneumonids and aphids disperse. Hence, while there may be common mechanisms underlying parasite LDGs, these sorts of differences may provide for insightful examination of the general factors influencing broad-scale diversity gradients.

Parasite latitudinal gradients in general

A large proportion of species on Earth are parasitic (de Meeus and Renaud 2002, Dobson et al. 2008, Poulin 2014) but we know relatively little about their geographical distributions (Poulin 2014). Most previous studies that have examined parasite distributions across latitudes have used data assembled from the limited literature on parasites and hosts belonging to different species at different latitudes (e.g., Gregory et al. 1991, Poulin 1995, Rohde and Heap 1998, Krasnov et al. 2004, Nunn et al. 2005, Lindenfors et al. 2007). The outcomes of these studies have been mixed, and this has been reflected in two reviews. Schemske et al. (2009) suggested a general trend of higher parasite richness and prevalence at low latitudes, while a meta-analysis by Kamiya et al. (2014) detected no overall effect of latitude on parasite species richness. These mixed results are likely at least partly a reflection of true differences between particular host–parasite groups. However, the lack of clear results is also likely due to variation in analytical methods and problems with underlying data, which are assembled from a limited literature. For instance, the tropics are often poorly represented, or not represented at all, which can preclude detection of LDGs (Willig et al. 2003). To cite two relevant examples, Poulin and Mouritsen (2003) detected that trematode richness appeared to increase with latitude across snail host species, and that the relationship disappeared after accounting for host phylogeny. Additionally, further, within-species analyses for the few snail species with sufficient compiled data found no LDG (Thieltges et al. 2009). However, as noted in both studies, the lack of tropical data makes it difficult to seriously evaluate latitudinal diversity gradients for parasites. However, even two comparative studies that did include some tropical data (Rohde and Heap 1998, Nunn et al. 2005) report mixed results. Hence, on the whole, we agree with Schemske et al. (2009) that available data are too limited to adequately understand how the LDG pertains to parasites, and note, along with Poulin (2014), that we may most effectively improve our understanding of parasite LDGs by undertaking studies of parasite diversity in widespread host species, as was done here.

To our knowledge, there has only been one previous study that examined the LDG for parasites of a single host species that naturally spans temperate to tropical latitudes. In their examination of human parasites,

Guernier et al. (2004) reported greater parasite richness in the tropics. In addition, humans appear to experience higher levels of infection by parasites in the tropics (Low 1990, Cashdan 2001). Although these results may be confounded by differences in wealth, the extent of public health programs across these regions, and geographic origins of human diseases, both patterns for humans are consistent with general latitudinal diversity and species interaction gradients. Our results run counter to what has been documented for humans, with parasite diversity being lower and interactions being weaker in the tropics. The differences in these two systems underscore that we can clearly benefit from additional studies of parasite diversity on widely distributed host species to better develop empirical generalizations and test mechanistic hypotheses concerning parasite LDGs.

Our study has focused on parasite communities infecting two widespread host species, and therefore cannot directly resolve the question of how overall parasite species diversity will vary with latitude. It has been reasonably postulated (e.g., Rohde 1992, Poulin 2014) that overall parasite diversity (total parasite species in all hosts per unit area) will increase in the tropics as a consequence of parasite diversity tracking host diversity (i.e., more host species equal more parasite species). Our documentation of reversed LDGs suggests that the situation will be more complex and may not follow a simple linear relationship. Specifically, although increasing host richness should tend to drive increased parasite diversity, this will be countered to the extent that parasite diversity is lower per host species. Hence, a thorough understanding of the relationship of overall parasite richness with latitude must account for the interplay of these two potentially antagonistic trends.

Conclusion

The two host–trematode systems that we examined exhibit latitudinal gradients in species diversity and interaction strength that are opposite to typical patterns. These reversed gradients are broadly interesting because the nature of the study system rules out explanations based on large-scale mechanisms, permitting a focus on more local ecological mechanisms. These trematode communities are amenable to further experimental studies testing general hypotheses concerning how local factors influence LDGs. Hence, the reversed LDGs documented here may be exceptions that help prove a general rule for the role that local factors have in driving LDGs. In general, parasite communities in widespread host species, perhaps even more widespread than the hosts studied here, could provide useful tools to understand the LDG and aid in deciphering the mechanisms that shape patterns of biological diversity.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/15-0518.1.sm